

## Article

# The Past Matters: Previous Management Strategies Modulate Current Growth and Drought Responses of Norway Spruce (*Picea abies* H. Karst.)

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**Abstract:** Due to high productivity and past management approaches, the forests of Central Europe are heavily dominated by conifers, even on sites where they do not occur naturally at all. One prominent example is Norway spruce (*Picea abies* H. Karst.), a species considered particularly vulnerable to severe droughts, especially outside of its ecological niche where it has been widely planted over the past centuries. In the face of global change, it is a major task for foresters to increase these forests' ability to cope with the impacts of increasing climatic extremes. Therefore, gaining more knowledge about how different management strategies affect the drought responses of trees is crucial. However, we still know little about the influence of the individual treatment history of a tree on its growth. We used a dendroecological approach to address this issue and to assess how initial spacing, structural diversity, tree size, and density regulation approaches modulate annual growth, especially in drought years. We hypothesized that stand establishment and past silvicultural treatment codetermine tree growth and drought resilience. Our study took place at the combined spacing-thinning trial Fürstenfeldbruck 612 (FFB 612) in Southern Germany, since it delivered precise long-term data covering a broad range of treatments. Based on linear mixed effect models, we showed that the individual treatment history of a tree affects its annual growth and drought responses considerably. In more detail, we found that (i) high structural diversity in the vicinity of each tree favored growth and improved a tree's performance under drought; (ii) larger trees were more climate-sensitive; (iii) previous high variations in thinning intensity, and consequently strong fluctuations in growth, affected current growth negatively and reduced recovery from droughts. Furthermore, we sought to understand the underlying mechanisms and to draw potential implications for refining silvicultural guidelines.

**Keywords:** thinning; spacing; drought response; resilience; recovery; resistance; ecological memory; structural diversity; Norway spruce (*Picea abies* H. Karst.)



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## 1. Introduction

Against the backdrop of climate change, heat waves and extreme droughts have increased in recent decades [1,2] and are expected to become more severe, prolonged, and frequent in the future [3,4]. These extremes are a socio-economic and environmental threat [5]. Forest ecosystems are considered particularly susceptible to climatic changes [6,7], since trees are long-lived and since quick acclimations to a changing environment are hardly possible. Drought stress can cause growth decline at tree [8] and stand level [9], alter tree allometry [10], or induce small-scale and large-scale tree mortality [11–13]. The growth responses of trees towards drought differ, amongst others, in terms of age [14], size [15–17], competitive situation [18], mixture [19,20], and species [21,22]. In Central Europe, Norway spruce (*Picea abies* H. Karst.) is considered a drought-intolerant species, which simulation studies [23,24], throughfall exclusion experiments [25], climatic envelope studies [26],

as well as dendroecological studies [27,28] have revealed in the past. A particularly high susceptibility to droughts has been observed outside its natural distribution range [22]. In previous centuries, however, N. spruce was planted extensively throughout Europe outside of its natural range, making it one of the most valuable tree species [29,30]. Despite changes in forest policy over recent decades, N. spruce still has a 25% share of forest land in Germany [31]. The ecological stability and the associated ecosystem services of those forests are now especially at risk [32], as a further build up in natural disturbances, as observed in recent decades, is expected [33,34]. As a result, the future profitability of N. spruce forests is associated with a high level of uncertainty [35]. Hence, silvicultural management options are needed that tackle predicted future challenges and adapt these forests to a changing climate. Converting monospecific, even-aged forests into mixed, uneven-aged stands is considered as a viable option [36] due to its many benefits [37]. This is, consequently, a focus of forestry policy in Germany [38]. However, there is also a demand for management recommendations to cope with present climatic extremes in pure conifer stands. One possible approach is to actively regulate competition between trees, since stand density is considered one of the main drivers determining growth [39]. A reduction in competition may positively affect the availability of soil water, light, and nutrients [40,41] due to changes in stand density and tree size distribution. Density reductions are suggested to improve water availability at dry sites [42], especially for isohydric tree species, such as N. spruce. When droughts occur, previous thinning activities can reduce mortality [43] and water stress [44], enhance resistance [45], and promote recovery and growth [46]. Thinning intensity [47,48] and frequency [49] have been shown to affect drought responses of conifers, with differences among site conditions [48]. However, adverse effects have also been observed. Heavily opening the canopy and reducing the stand density may disturb the stand climate [50] due to changes in solar radiation and wind speed [40], possibly leading to a higher transpiration and evaporation [51]. In addition, forest floor vegetation may be promoted [52], increasing the competition for water.

Thus, different forest management approaches may codetermine the trees' performance in droughts. It has been hypothesized that the management history and past environmental conditions may be retained as a kind of an ecological memory within each tree [53], reflected by its tree-ring pattern [54], past growth trajectory [53], or crown morphology [55], that may influence future growth. However, there are still gaps in our knowledge. Our overarching hypothesis was that the type of stand establishment and the past silvicultural treatment codetermine annual growth and response to drought. For that reason, our study focused on disentangling the influence of past competition, growth variation, initial spacing, tree size, and treatment strength and frequency on current growth under drought stress.

We relied on the concept of resilience to assess the ability of trees to cope with drought stress. Since several definitions exist [56,57], we focused on the tree-level concept of resilience proposed by Lloret et al. [14], which is split into three complementary indices: resistance, recovery, and resilience. In recent years, these indices have been widely used in dendroecological studies [57]. We used tree-ring data because their patterns can be considered as a type of an integrated archive for reflecting environmental conditions [58,59] and are, therefore, an adequate tool to capture growth responses to climatic extremes, such as drought.

Our study was based on the combined spacing and thinning trial in N. spruce Fürstentfeldbruck 612 (FFB 612) in Southern Germany. The trial was initiated in 1974 by the International Union of Forest Research Organizations (IUFRO) [60]. Since such long-term experiments comprise detailed data about the effects of thinning and stand density [61], FFB 612 was appropriate for addressing the following questions:

Q1: How did previous management strategies affect annual growth at the combined spacing and thinning trial FFB 612?

Q2: How have past silvicultural treatments affected drought responses at present?

## 2. Materials and Methods

### 2.1. Study Site and Experimental Design

To disentangle how the individual history of a tree influenced its current growth and affected its growth reactions towards drought, we chose the combined spacing-thinning trial Fürstenfeldbruck 612 (FFB 612). The experiment was initiated in 1974 by the International Union of Forest Research Organizations (IUFRO) and is part of a series of long-term experiments across Europe. FFB 612 is a pure, even-aged N. spruce stand that originated from a plantation with four-year-old saplings after the previous stand had been severely damaged by wind.

The site is 40 km west of Munich in southern Germany at 11.05° E longitude and 48.14° N latitude and an elevation of 550 m a.s.l. The region is characterized by a mild oceanic climate with a mean annual temperature of 8.8 °C (14.7 °C in the growing season) and an annual precipitation of 932 mm (575 mm in the growing season) over the past 30 years. It belongs to the Landsberg am Lech forestry enterprise and is part of the ecodistrict 13.5 Landsberger Altmoräne. The natural vegetation is described as submontane European beech-silver fir forests with sparsely interspersed N. spruce [62]. The prevalent soils are Lessivé soils on Loess substrate. Spruce is particularly vigorous on these sites due to the site conditions. The selected stand can be assumed to be representative for planted pure spruce forests in the Alpine foothills. Since its establishment in the 1970s, the temperature has increased by about 2 °C, while annual precipitation has declined slightly, resulting in progressively drier conditions in recent years (see Figure 1).

The trial has a total size of 3.36 ha and consists of 21 rectangular plots covering a broad range of treatments, differentiated by thinning intensities and the initial spacing. Each plot has a size of 900 m<sup>2</sup> with an additional buffer zone, resulting in a total plot size of 1600 m<sup>2</sup>, whereas each buffer zone was treated the same as the corresponding plot. In total, ten different thinning-spacing combinations were realized. The plot design is visualized in Figure 2. Since its establishment in 1974, all the trees, except the buffer zone, have been measured seven times, the first time in spring 1992, followed by surveys in 1996, 2001, 2006, 2012, 2017 (all autumn), and 2021 (spring). Each survey covered the measurement of the diameter at breast height ( $dbh_{1.3}$ , cm) as well as the height of 30 trees per plot. In addition, each tree was allocated a number, and the stem position was recorded at the beginning. Trees were only harvested in years with surveys, except for trees that died off naturally due to wind or competition, for instance. Those trees were removed due to pest control. Because plots were only treated in survey years, it was possible to observe detailed changes in stand composition. In general, the experiment is guided by a uniform treatment concept. At the end of the rotation period, 300 trees ha<sup>-1</sup> (thinning trial), respectively 400 trees ha<sup>-1</sup> (spacing experiment), are pursued. However, the way to get there is different for each treatment method. Thinnings on most plots follow set curves for tree number–top height relationships. Exceptions are plot numbers 8 and 21, which follow a defined tree volume removal and plots 7 and 19, which remain unthinned. A detailed overview is given in Table 1. Further insight can be obtained in Pretzsch [63], Rötzer and Pretzsch [64], Huang and Pretzsch [65], and Jacobs et al. [66].

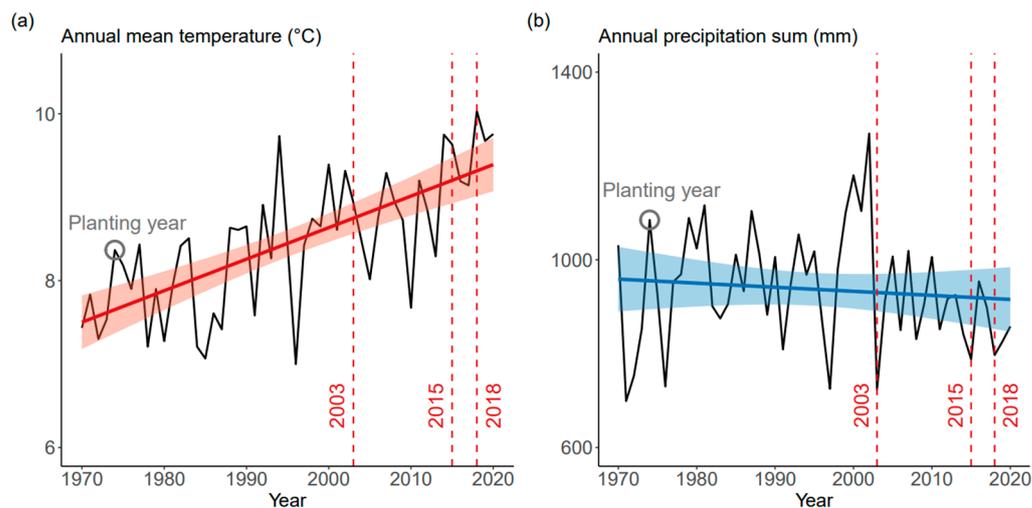
### 2.2. Dendrochronological Measurements

Field work took place in December 2020. We sampled 78 N. spruce individuals using a HAGLÖF increment borer with a core diameter of 5 mm (Haglölf, Sweden). We relied upon standard dendrochronological techniques to obtain annual ring widths [58,68]. Trees for coring were selected from the buffer zone to avoid damaging trees within the plots and thus affecting future surveys at the study site. This was possible since the buffer zone has always been treated in the same way as the neighboring plot. To prevent boundary effects on our sample trees, we only chose trees with at least one additional planting row as an additional buffer to the plot margin. Further, we only selected trees that had no obvious signs of damage, disease, or bark beetle infestations. In total, trees were cored from three different initial spacing levels (2.5 m × 1.6 m; 4 m × 2.5 m; 5 m × 5 m), resulting in six different

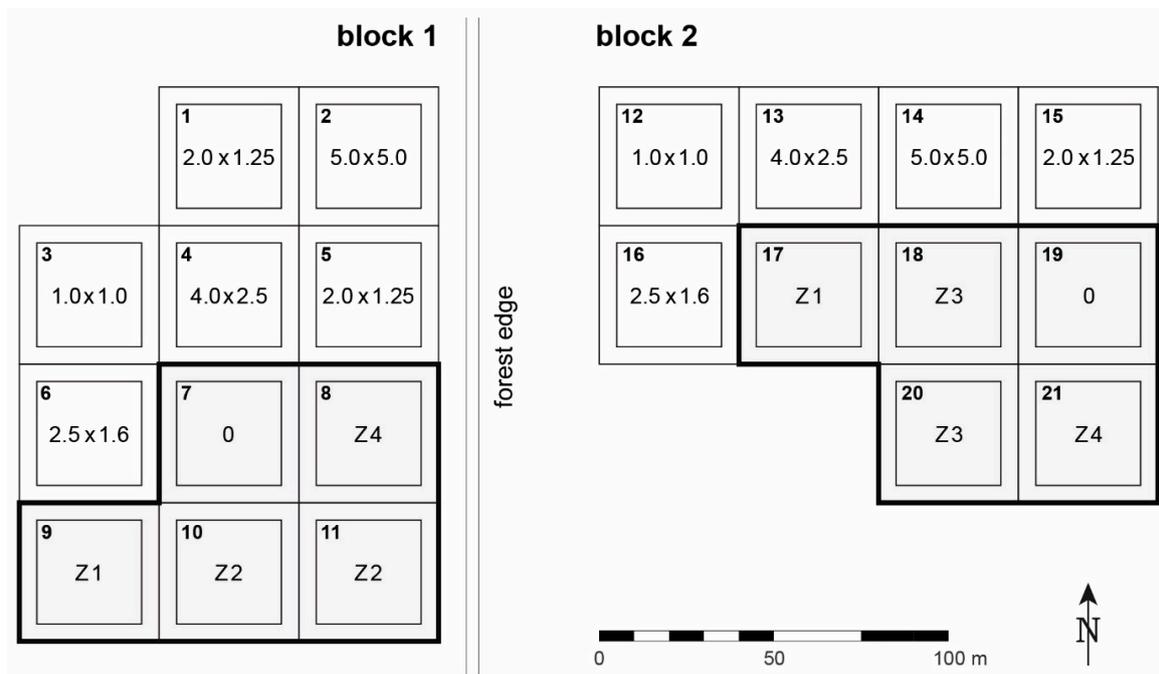
thinning/spacing combinations (see bold marked plot numbers in Table 1). To minimize influences of reaction wood and to obtain representative tree ring series, we took two cores from each tree at breast height ( $dbh_{1.3}$ ) in the north and east cardinal directions [19]. We attempted to hit the center of the stem to cover as many growth rings as possible, resulting in 156 extracted increment cores. They were air-dried, mounted, and glued on wooden supports and subsequently sanded using sandpaper with a progressively finer grit (120 to 400 grit) to enhance the visibility of tree rings. Ring widths were measured to the nearest 1/100 mm using a digital positioning table (LINTAB series 5) and the TSAP-WIN software (both RINNTECH Heidelberg, Germany). Cross-dating accuracy was first inspected visually [69] by considering pointer years with extraordinary narrow rings, common to most tree ring series [70]. The years 2003, 2015, and 2018 turned out to be the most helpful. Afterwards, cross-dating was verified statistically using the program COFECHA [71].

**Table 1.** Detailed information on the realized spacing and thinning variants. A = spacing trial; B = thinning trial (IUFRO). Plot number and variant name columns refer to the study design presented in Figure 2. Bold plot numbers indicate plots where tree cores were taken from the buffer zone. The second column reflects the initial tree number per hectare when planted in 1974. In the other columns, the staggered thinnings are listed. For each thinning, the remaining number of trees, respectively the remaining volume, is displayed per hectare. The letters *c* and *b* listed behind represent the thinning methods used: *c* = crop tree thinning, *b* = thinning from below, or *c, b* = combination of both.

Plot Number	Initial Tree Number (ha <sup>-1</sup> )	Variant Name	Cored Trees	Thinning at $t_0$							
				12 m (1991)	15 m (1996)	21 m (2006)	25 m (2012)	27.5 m (2017)			
<b>A</b>	<b>3, 12</b>	10,000	1 × 1	5000	2500	2000	1000	500	<i>c, b</i>	<i>c, b</i>	<i>c, b</i>
	1, 5, 15	4000	2 × 1.25	3000	1500	1200	700	500	<i>b</i>	<i>c, b</i>	<i>c, b</i>
	6, 16	2500	2.5 × 1.6		1000	800	500	300		<i>c</i>	<i>c, b</i>
	4, <b>13</b>	1000	4 × 2.5	18	500	400	300		<i>c</i>	<i>c</i>	
	2, <b>14</b>	400	5 × 5	12	300	200			<i>b</i>		
<b>B</b>	<b>7, 19</b>	2500	0	18							
	9, 17	2500	Z1		1200	700			<i>c, b</i>	<i>c, b</i>	500
	<b>10, 11</b>	2500	Z2	15	1200		900	700	<i>c, b</i>	<i>c</i>	500
	18, <b>20</b>	2500	Z3	6		1200	900	700	<i>c, b</i>	<i>c</i>	500
	8, <b>21</b>	2500	Z4	9		80 m <sup>3</sup> ha <sup>-1</sup>	80 m <sup>3</sup> ha <sup>-1</sup>	700	<i>c, b</i>	<i>c, b</i>	500



**Figure 1.** Temperature (a) and precipitation (b) development from 1970–2020 at the study site. Climate data were obtained from the 1 km × 1 km grid of the DWD Climate Data Center [67]. The dashed lines highlight the drought years considered in this study.



**Figure 2.** Study design of Fürstenfeldbruck 612 (FFB 612). The trial includes ten different spacing–thinning combinations in two blocks, comprising 21 equally sized, rectangular plots, each bordered by a buffer zone. Plots that are surrounded by thin lines differ regarding their initial spacing (spacing trial; 1.0 m × 1.0 m, 1.25 m × 2.0 m, 1.6 m × 2.5 m, 2.5 m × 4.0 m, 5.0 m × 5.0 m), whereas bold framed plots vary only in their thinning regime (thinning trial), having an initial spacing of 1.6 m × 2.5 m. The buffer zone was consistently treated similarly to the neighboring plots.

### 2.3. Calculation of Basal Area Increment

For further analysis, the two ring-width series per tree were averaged to obtain a representative growth trajectory for each tree. Subsequently, the different ring-width series per tree were transformed to basal area increments ( $bai$ ,  $\text{cm}^2$ ) using the formula:

$$bai_t = \pi * (r_t^2 - r_{t-1}^2), \quad (1)$$

where  $r$  is the radius of the tree at breast height and  $t$  the year of tree ring formation. Basal area increment was preferred over ring width data because it is known to capture the biomass increment of a tree better [72,73] and is less dependent on tree size and cambial age [74].

### 2.4. Quantification of a Tree's Current and Past Competition

Our overarching goal was to combine a tree's annual growth with its individual competition history. However, only the annual growth from trees from the buffer zone was available and, contrary to that, the periodic measurements from the trees within the plots, which were required to calculate competition metrics. To overcome that issue, we applied a procedure that we further refer to as “pairing.” For this purpose, we compared the growth of the cored trees with that of the trees in the plots. The best match was sought and was determined using the lowest sum of squares between the growth trajectories of the trees. Finally, tree data gained from the surveys were extracted and assigned to the respective matching tree from the buffer zone. For a detailed explanation of the pairing process, see Appendix A “Description of the Pairing Process.”

Since 1992, the surveys have delivered repeated, precise measurements that allow for the quantification of competition. Here, we refer to the competitive status at the beginning of each year. Due to the periodic surveys, tree or competition data were only available for

seven points in time (1992, 1997, 2002, 2007, 2013, 2018, and 2021). To obtain annual values of competition, we assumed that competition between surveys increased linearly. This assumption can be made because trees were only logged in survey years and immediate changes in stand composition resulting from this can be still observed. Based on the tree data gained through the pairing process, we derived several metrics that try to describe the individual competition history and the latest status of every single tree in a given year. The calculated metrics are defined below.

#### 2.4.1. Competitive Status

For determining the competitive status in each survey year, we calculated the local stand density index (*sdi*), according to Reineke [75]. The local *sdi* is distant-dependent and is therefore well suited to adequately reflect the competitive situation of a tree [76,77]. Due to its easy interpretation [78], it was chosen over other competition indices. To quantify the local *sdi*, all trees within the search radius, *sr*, except the central tree, were used to calculate the local density *n* on circle area *a*.  $N = 10.000/a \times n$  was the respective tree number upscaled to one hectare [79]. For the *n* trees, we calculated the quadratic mean stem diameter  $d_q$ . Based on *N* and  $d_q$ , we then calculated the local density,

$$sdi = N \times (25/d_q)^\alpha, \quad (2)$$

around each individual tree. The local *sdi* was calculated using the species-specific allometric exponent of  $\alpha = -1.664$  derived by Pretzsch and Biber [80]. Note that this exponent  $\alpha$  was derived on unthinned plots of long-term experiments in South Germany located in the same area as FFB 612. The used exponent  $\alpha = -1.664$  deviated from the species-overarching exponent of  $-1.605$ , as proposed by Reineke [75]. The radius around a tree, where trees were considered to be competitors, was chosen flexibly depending on its height. Hence, the search radius *sr* around each tree *i* was defined as  $sr_i = h_i \times 0.25$ , where *h* is the individual tree height. The higher the local *sdi*, the higher was the competition. A value of zero indicated that no trees were within the defined search radius. Since only the height of 30 trees per plot and survey was measured, missing tree heights had to be modeled. Based on available data for diameter at breast height (*dbh*) and tree age (*age*), we used the following formula to model the missing tree heights (*h*):

$$\ln(h) = a_0 + a_1 \times \ln(dbh) + a_2 \times \ln(age) + a_3 \times \ln(dbh) \times \ln(age) \quad (3)$$

The model, as well as all regression coefficients, were significant at the level of  $p < 0.001$  ( $n = 4372$ ,  $R^2 = 0.91$ ). To account for a possible edge bias at the plot boundaries, we conducted a toroidal shift of each plot before calculating the competition metrics. To perform this, detailed information on stem positions and tree dimensions per plot were copied and placed, respectively, at all eight possible directions of the plot periphery of the original plot [81,82].

#### 2.4.2. Competitive History and Release

To represent the influence of the initial spacing in 1974, we calculated the growing area of each tree *initfl* based on initial spacing patterns (1.6 m × 2.5 m, 2.5 m × 4.0 m, 5.0 m × 5.0 m), resulting in three different levels: 4 m<sup>2</sup>, 10 m<sup>2</sup>, and 25 m<sup>2</sup>. Based on the local *sdi* calculations (see Section 2.4.1), several other metrics were derived that aimed to describe changes in competition and growth developments in the past. First, the mean density level under which a tree has grown is given by *meansdi*. High values indicated a high level of density around the tree, and low values indicated the opposite. The index  $\Delta sdi$  described how competition changed from one year to another and, thus, captured both increasing competition from growth and competition release caused by logging. The higher the  $\Delta sdi$  the stronger was the change in competition. Negative values indicated competition release and vice versa. Further, *cvarsdi* and *cvar $\Delta sdi$*  were calculated by determining the coefficient of variation of *sdi* and  $\Delta sdi$ , respectively. They represented the intensity and

frequency of thinnings. High values of *cvarsdi* implied repeated strong treatments, whereas low values reflected a continuous development of competition without abrupt changes. The metric *cvar $\Delta$ sdi* gave information on the variation in thinning strength. Here, high values indicated a strong variation in density reduction. The index *sditrend* was applied to capture different treatment strategies, e.g., no thinnings at the beginning and strong interference later. To describe changes in treatment strategy, the time frame before a specific year was split in two; the *meansdi* was computed for each half. The ratio between the second half and the first half resulted in the *sditrend* metric. A value >1 implied an increasing stand density over time, while a value of <1 indicated a decrease in competition, suggesting a high density first with strong thinnings later. Furthermore, we calculated the metric *cvarbai* to scrutinize the influence of past growth variation on current growth. It is defined as the coefficient of variation of the basal area increments of a particular tree. High *cvarbai* values indicated a strong growth variation in the past, whereas a small *cvarbai* represented a more uniform growth course [53,83]. Last, to characterize the structural diversity (*strudiv*) in the vicinity of each tree, the coefficient of variation of the stem diameters from the competitors within the search radius was derived. The higher the *strudiv*, the higher the structural diversity of the stand within the vicinity of the respective central tree.

### 2.5. Climate Data and Drought Identification

Climate data were available on a 1 km  $\times$  1 km grid from the German National Weather Service [67]. We obtained monthly data of mean, maximum, and minimum temperature and precipitation for the period 1980–2020. We applied the Standardized Precipitation and Evapotranspiration Index (SPEI) [84] to classify climatic conditions and identify drought years. We relied on this index as it considers the effects of high temperatures and thus, increased evapotranspiration, which is of growing importance considering global change. To calculate SPEI, we derived potential evapotranspiration (PET) using the Hargreaves equation [85,86]. According to Bhuyan et al. [87], the SPEI from March to August (SPEI6) best reflects the impact of drought on the growth of N. spruce in regions with mild oceanic climates. Moreover, this period also covers the duration of cambial activity of N. spruce in Central Europe [88]. Hence, we chose that period for further analysis. Following Slette et al. [89], we defined droughts as years with extremely dry (SPEI6  $\leq -2$ ) or severely dry ( $-2 < \text{SPEI6} \leq -1.5$ ) conditions in the vegetation period. Two droughts have been identified in the past 30 years based on this definition. First was the extreme drought in 2003 (SPEI6 =  $-2.3$ ), followed by the recent drought of 2018 (SPEI6 =  $-2.0$ ). Despite its slightly less SPEI value (SPEI6 =  $-1.4$ ), we also considered 2015 a drought year, because it was characterized by a dry late summer, not fully reflected by the SPEI6. Besides, tree ring analysis revealed remarkably small ring widths that year.

### 2.6. Quantification of Growth Reactions on Drought

To unravel the possible influences of each tree's individual past on its response to drought, we applied several indices to quantify these growth reactions. Accordingly, we used the indices resistance (*Rt*), recovery (*Rc*), and resilience (*Rs*), as proposed by Lloret et al. [14]. These indices were defined as follows:

$$R_t = \frac{bai_{Dr}}{bai_{preDr}} \quad R_c = \frac{bai_{postDr}}{bai_{Dr}} \quad R_s = \frac{bai_{postDr}}{bai_{preDr}} \quad (4)$$

where *bai<sub>Dr</sub>* is the basal area increment (*bai*, cm<sup>2</sup>) in the drought year itself, *bai<sub>preDr</sub>* is the average growth in a chosen period of two years before the drought event, and *bai<sub>postDr</sub>* is the average growth in the two subsequent years after drought. The lower *Rt* was, the lower the resistance was, whereas a value of 1 indicated that the tree showed no particular response towards drought and, respectively, captured that the tree was resistant. *Rc*, on the other hand, described the ability to recover from drought in the subsequent years. If *Rc* < 1, the trees did not recover from the drought stress, and instead they further declined in terms of growth. Vice versa, a value of >1 implied recovery to a certain degree. Last, resilience (*Rs*)

reflected the ability to reach the growth-level before the drought again. Values greater than 1 indicated that the trees reached higher growth than before the pre-drought period, hence full recovery. Contrary, a resilience of <1 suggested a prolonged growth decline following drought stress. Since the pre-drought period of 2018 overlapped with the post-drought period of 2015, we only considered the drought years 2003 and 2015 for further analysis. A detailed explanation regarding the exclusion of the 2018 drought from our analysis and the selection of input data and length of pre-drought and post-drought periods can be found in the Appendix. See Appendix B “Quantification of Drought Responses” for a detailed description.

### 2.7. Modeling Approach

We applied linear mixed effect models that account for nesting in the data and avoid overly progressive significances due to pseudo-replication to answer the two research questions posed. We only used weakly correlated predictors ( $r \leq 0.5$ ) for the analysis [90] and assessed (multi-) collinearity by considering variance inflation (*VIF*). Variables exceeding the threshold of  $VIF > 2$  were excluded from the model. Further data exploration was performed following suggestions by Zuur et al. [91]. A global model with two-way interactions was created, whereas random effects and correlation structures were incorporated. Under consideration of biological plausibility, potential final models, nested in the global model, were selected based on the ranking of the second-order Akaike Information Criterion (*AICc*) [92]. The selection was supported with the help of an automated model selection procedure [93]. This process revealed the best models based on the lowest *AICc* values with a delta less than 2. Akaike weights were computed to add multi-model inference and help with model selection uncertainty [92]. Model assumptions were checked by plotting residuals versus fitted values and versus each explanatory variable. Where applicable, we assessed the residuals for temporal dependencies [94]. We considered all years between 1992 and 2020 to check whether the metrics characterizing previous management strategies affected tree growth (Q1). The global model included the log-transformed annual basal area increment (*bai*, cm<sup>2</sup>) as the response variable. The fixed covariates were *SPEI6*, *sdi*,  $\Delta sdi$ , *cvar* $\Delta sdi$ , *strudiv*, *cvarbai*, the log-transformed *basal area* (all continuous), and *initfl* (categorical). The final model, resulting from the automated model selection procedure, included all initial covariates, except  $\Delta sdi$ , as well as *SPEI6* \*  $\ln(\text{basal area})$  and *SPEI6* \* *sdi* interactions.

$$\ln(bai_{ij}) = a_0 + a_1 * \ln(\text{basal area}_{ij}) + a_2 * SPEI6_j + a_3 * sdi_{ij} + a_4 * strudiv_{ij} + a_5 * cvar\Delta sdi_{ij} + a_6 * cvarbai_{ij} + a_7 * initfl_i + a_8 * SPEI6_j * sdi_{ij} + a_9 * SPEI6_j * \ln(\text{basal area}_{ij}) + b_i + \varphi + \varepsilon_{ij}, \quad (5)$$

where  $bai_{ij}$  represented the basal area increment in year  $j$  of tree  $i$ , and  $i = 1, \dots, 78$ . The terms  $a_0$ – $a_9$  were the regression coefficients of the fixed effects. The variable  $b_i$  represented the random effect related to the intercept  $a_0$  and accounted for the nested data structure, as multiple metrics were measured or computed for the same tree. Normal distribution and constant variance were assumed ( $b_i \sim N(0, \sigma^2)$ ). Despite accounting for the random tree effect, temporal autocorrelation was still detected. To incorporate the temporal dependency among observations per tree, an autoregressive correlation structure (AR1,  $\varphi$ ) was included [94]. Last, the error term  $\varepsilon_{ij}$  was expected to be normally distributed with constant variance and a mean of zero.

To answer the initial question of whether the individual past of a tree had any influence on its growth response towards years with remarkably dry conditions (Q2), we built three global models, each with a different response variable (resistance, recovery, or resilience) but with the same predictors and interactions. To describe the individual past of each tree, *cvar* $\Delta sdi$ , *meansdi*, *cvarbai*, and *sditrend* were incorporated as covariates, while *strudiv* was included to delineate the current situation in the vicinity. The categorical predictor year was also added to identify differences between drought events. Furthermore, the *basal area* also formed part of the model. The final models are stated as follows:

## Resistance

$$\ln(rt_{ij}) = a_0 + a_1 * \ln(\text{basal area}_{ij}) + a_2 * \text{year}_j + a_3 * \text{strudiv}_{ij} + a_4 * \ln(\text{basal area}_{ij}) * \text{year}_j + b_i + \varepsilon_{ij}, \quad (6)$$

## Recovery

$$\ln(rc_{ij}) = a_0 + a_1 * \text{year}_j + a_2 * \text{cvarbai}_{ij} + b_i + \varepsilon_{ij}, \quad (7)$$

## Resilience

$$\ln(rs_{ij}) = a_0 + a_1 * \text{year}_j + a_2 * \text{cvarbai}_{ij} + a_3 * \text{strudiv}_{ij} + a_4 * \text{year}_j * \text{cvarbai}_{ij} + b_i + \varepsilon_{ij}, \quad (8)$$

where  $rt_{ij}$ , respectively,  $rc_{ij}$  or  $rs_{ij}$  were the log-transformed drought index values from the drought year  $j$  ( $j = 2003, 2015$ ) identified for each tree  $i$  ( $i = 1, \dots, 78$ ). The meaning of the remaining formulae is equivalent to that of Equation (5).

We used the R version 4.0.3 [95] statistical software for all analyses and calculations. Specifically, we used the packages dplR [96], nlme [97], SPEI [98], rgdal [99], rdwd [100], car [101], effects [102], ggpubr [103], RColorBrewer [104], MuMIn [93], and the meta-package tidyverse [105].

### 3. Results

#### 3.1. Course of Growth

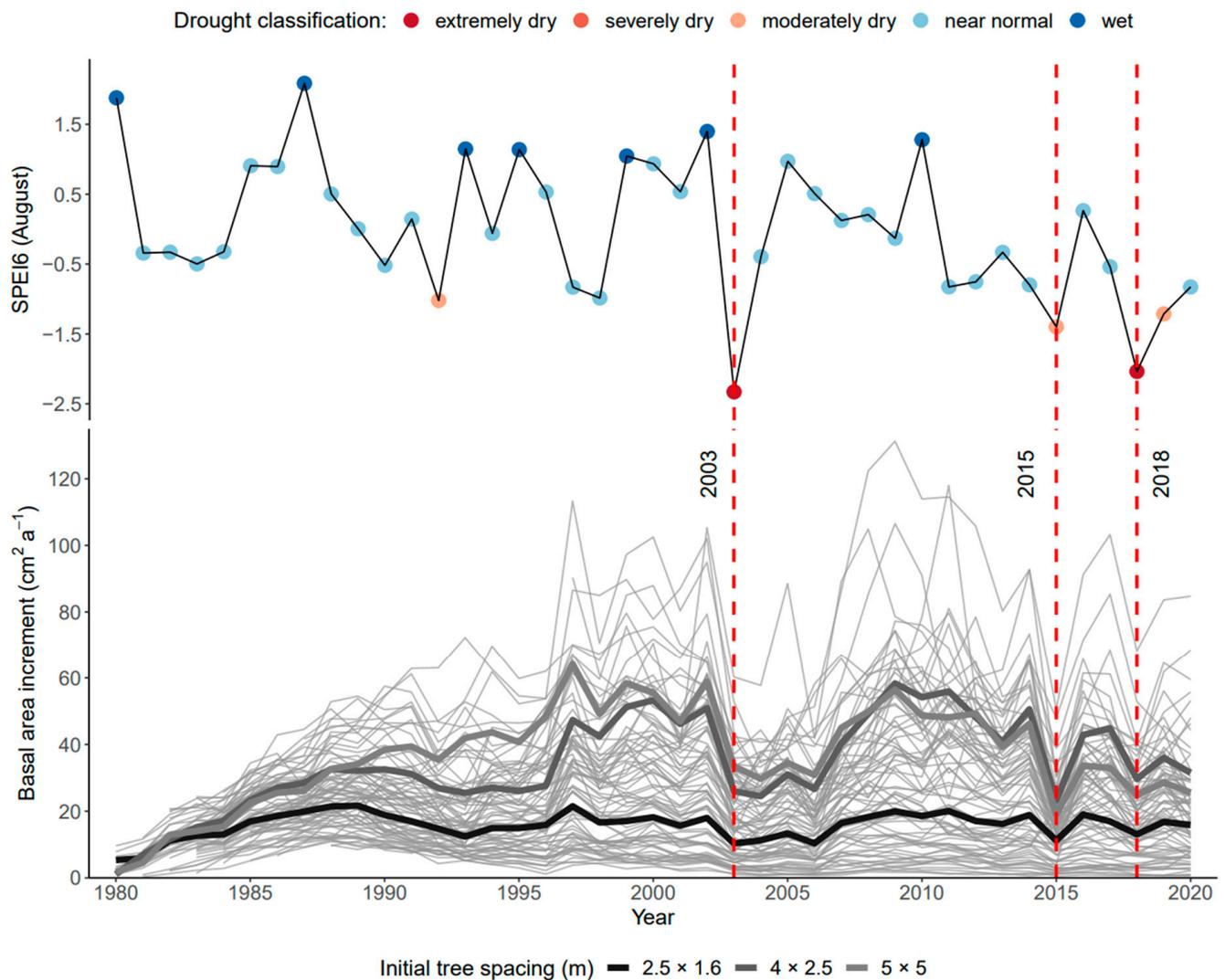
Differences in tree growth were observed between 1980 and 2020 (Figure 3). The initial spacing pattern determined the growth rates over the long term. Annual growth was greater for trees with a large initial spacing, due to the reduction in competition right from the start. Between 1990 and 2010, growth was highest for individuals with the widest initial spacing pattern of  $5 \times 5$  m. However, this changed in the last decade when a general decline in growth was noted for trees growing at lower stand densities. From that point on, trees with an initial spacing of  $10 \text{ m}^2$  had the highest growth rates. Intermediate growth increases, such as in 1997 or 2007, showed that release felling during the previous autumn (1996, 2006) accelerated subsequent growth. Due to differences in initial spacing and thinning frequency and intensity, the stem diameter at breast height varied between 14.0 cm and 55.9 cm when cores were taken.

#### 3.2. Effects of Climate, Tree Size, and Silvicultural Treatment History on Annual Growth (Q1)

Statistical analysis of the obtained data revealed that the annual growth of a tree during the period 1992–2020 was driven by its basal area, the given climatic conditions, its initial spacing in 1974, the structural diversity of surrounding trees, its current competitive situation, as well as its variation of growth and competition in the past. Table 2 presents the parameter estimates of the best model resulting from the multi-model comparison. Tree size was an important growth driver (positive effect; +). Furthermore, we were able to demonstrate significant differences in tree growth regarding initial stand densities (positive effect of wider stand densities; +). Tree growth was highest for trees planted in a  $4 \times 2.5$  m pattern. In general, the given climatic situation, represented by the SPEI6 (August), had a major impact on growth. The drier the weather, the lower the growth and vice versa. Years with particularly dry conditions, indicated by the red color coding in Figure 3 (color intensity reflects the severity of drought), caused setbacks in growth. The most severe impacts came from droughts in 2003 and 2015.

Significant interactions between SPEI6 and tree size showed greater sensitivity of larger trees to water supply ( $p < 0.001$ ). On the other hand, small trees were not or were only slightly affected by droughts. In addition, the fitted model suggested that a wider diameter distribution of competitors growing in proximity favored the growth of the tree

in question (+). Besides, the metrics that focused on describing the individual history of a tree indicated a significant negative relation towards annual increment. The more the trees varied in their previous growth ( $cvar_{bai}$ ), and the more the changes in competition ( $cvar_{\Delta sdi}$ ) fluctuated, the less the trees grew, whereas the differences were consistently more pronounced for larger trees. Model predictions are visualized in Figure 4.

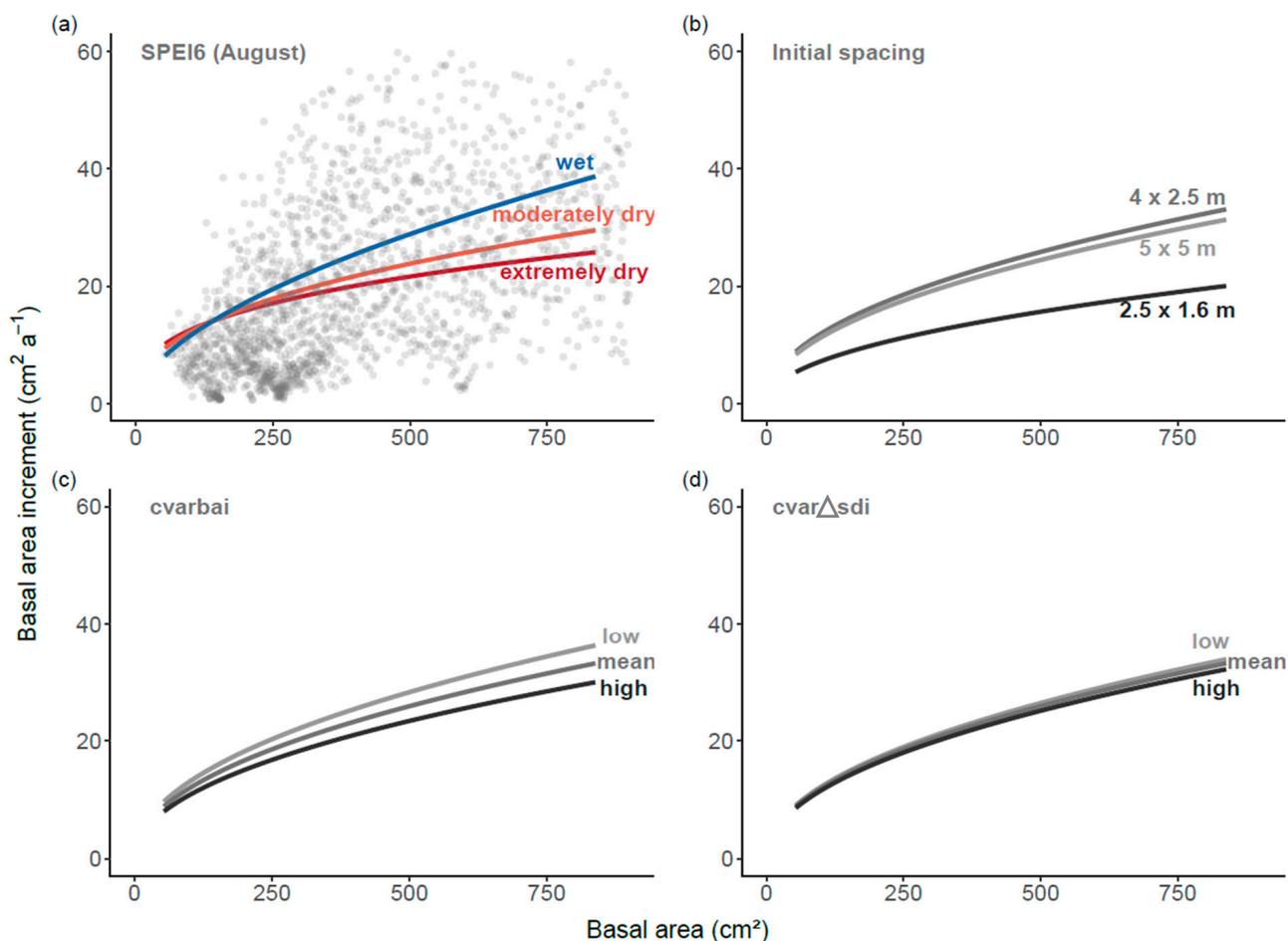


**Figure 3.** Below, the course of the basal area increment ( $\text{cm}^2$ ) of each cored tree ( $n = 78$ ) is shown. The bold lines represent the respective averages, whereas the different shades of gray highlight different initial spacing levels. Above, the progression of the SPEI6 in August is illustrated. The color coding refers to the drought classification by Slette et al. [89]. The dotted red lines accentuate the identified drought years based on SPEI6 and pointer years.

### 3.3. Influence of Ecological Memory, Respectively Management History, on Drought Response (Q2)

Regarding the droughts identified, N. spruce trees showed considerable differences in their growth response (see Figure 5 and Table 3). In the first severe drought in 2003 (SPEI6 =  $-2.33$ ), all trees showed a setback in growth compared to their previous growth. In 2015 (SPEI6 =  $-1.4$ ), however, the trees responded less uniformly. While the annual increment decreased significantly for most trees, some showed higher growth rates. In response to the 2003 drought, the trees indicated a lower average resistance ( $\bar{O} 0.59$ ) than in 2015 ( $\bar{O} 0.65$ ), highlighting the severity of the first drought. In the two years following the drought stress, trees recovered differently depending on the drought year. The trees recovered better from the drought in 2015, and some even exceeded the growth level

before the drought. In contrast, most trees barely recovered from the 2003 drought in the following two years. Our statistical analysis (for details see Table 3) revealed that resistance in 2015 was significantly affected by tree size (negative effect;  $-$ ). However, as indicated in Figure 6a, no size-specific trend was observed in 2003. Furthermore, our fitted model indicated that the greater the structural diversity in a tree's environment, the greater its resistance. Tree recovery was mainly determined by their past growth variability, with differences between drought years ( $p < 0.001$ ). As shown in Figure 6b, large growth fluctuations impaired recovery (see also Table 3,  $-$ ). In general, trees recovered better in 2015. Finally, results from the fitted model showed that previous growth fluctuations and structural diversity played an important role in drought response, with differences between the respective years ( $p < 0.01$ ). In both drought years considered, high structural diversity favored resilience. However, the trend was less clear for *cvarbai*. High growth variation negatively affected resilience in 2003, which had not been observed in 2015 (see Figure 6c).



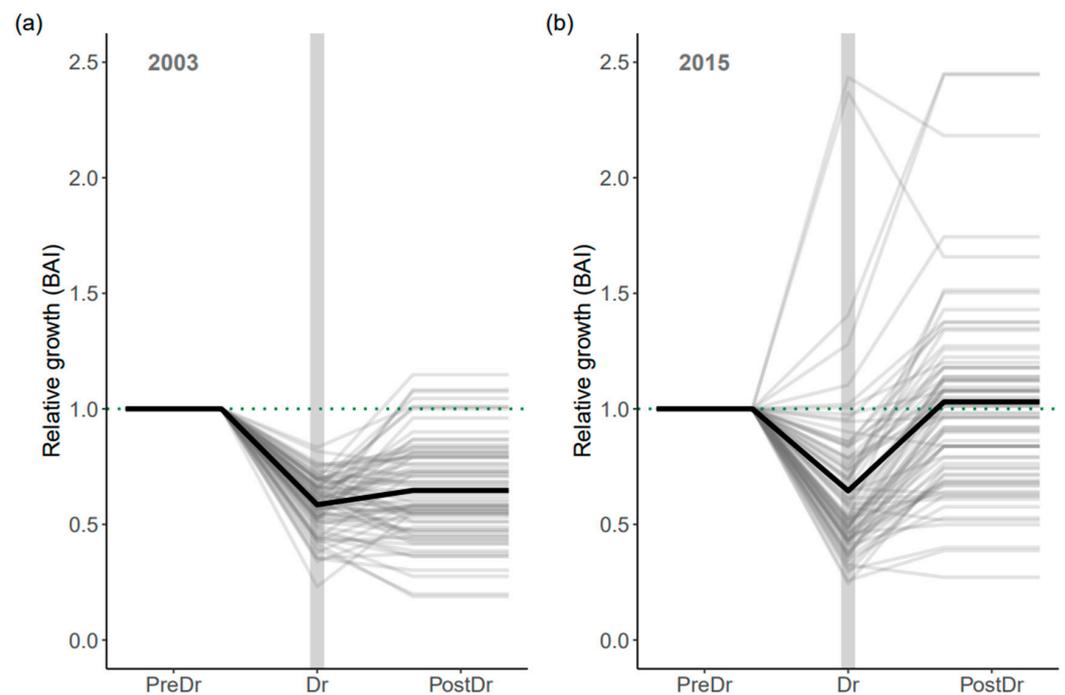
**Figure 4.** Effects of climatic conditions (a), initial spacing in 1974 (b), variation of previous growth (c), and of past changes in competition (d) on annual growth (y-axis). Each variable was predicted independently, while other variables were set to mean. For the categorical variable “initial spacing,”  $4 \times 2.5$  m was chosen to predict other variables. The x-axis represents the range of basal area ( $\text{cm}^2$ ) where 95% of the observations are located. These are exemplarily shown as gray dots in (a). The predictions for SPEI6 are based on the classifications by Slette et al. [89]. The chosen prediction levels for *cvarbai* and *cvar $\Delta$ sdi* correspond to the mean and the respective upper and lower quantiles based on bootstrapping with 1000 iterations. The labels refer to the actual values (e.g., low = low values of *cvarbai*).

**Table 2.** Parameter estimates of the growth model for the period 1992–2020 (see Equation (5)):  $\alpha$  are the regression coefficients of the fixed covariates;  $b$  represents the random intercept;  $\varepsilon$  is the error term;  $\varphi$  is the autoregressive parameter estimate accounting for temporal correlation.  $N_{tree}$  describes the amount of examined trees and  $N_{bai}$  the number of observations of the response variable. Significance levels: \*\*\* = 0.001, \*\* = 0.01, ° = 0.1.

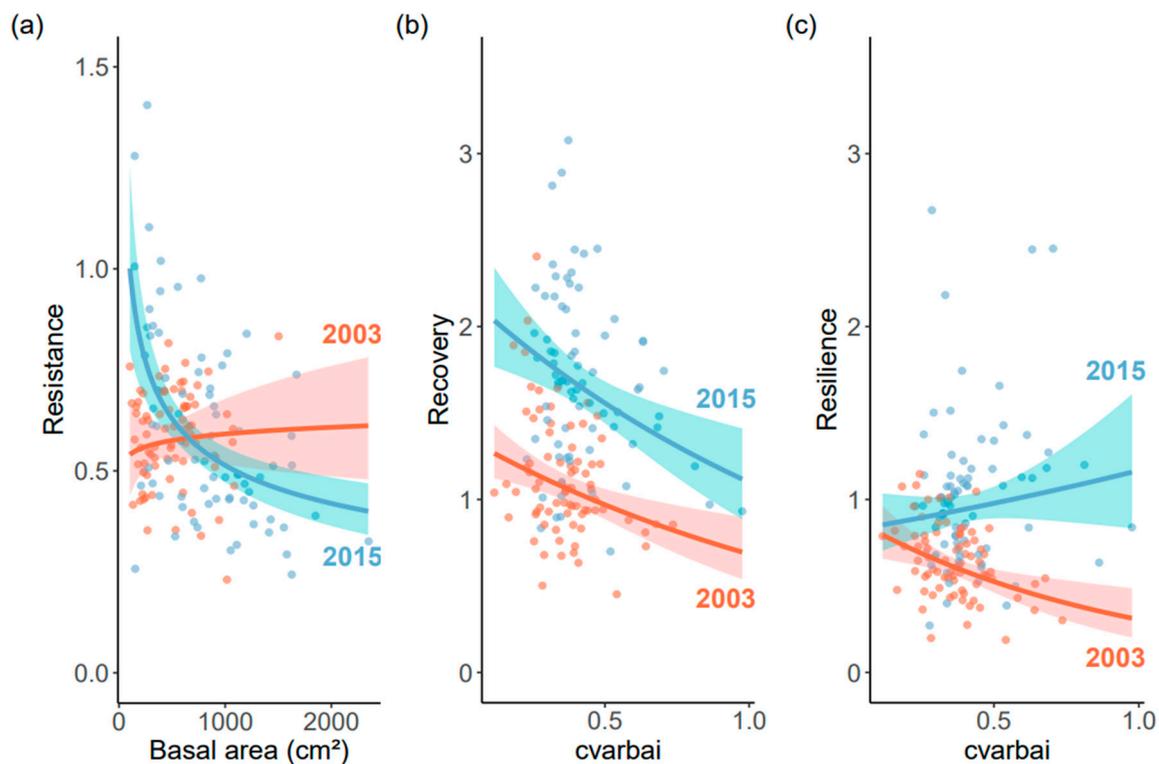
Annual Basal Area Increment [cm <sup>2</sup> a <sup>-1</sup> ]		
Fixed Effect Variable	Fixed Effect Parameter	Estimate (se)
<i>intercept</i>	$\alpha_0$	0.51 (0.27) °
<i>ln(basal area)</i>	$\alpha_1$	0.49 (0.05) ***
<i>SPEI6</i>	$\alpha_2$	−0.43 (0.05) ***
<i>sdi</i>	$\alpha_3$	<−0.001 (<0.001) ***
<i>strudiv</i>	$\alpha_4$	0.45 (0.17) **
<i>cvarΔsdi</i>	$\alpha_5$	−0.06 (0.02) **
<i>cvarbai</i>	$\alpha_6$	−1.16 (0.20) ***
<i>initfl10</i>	$\alpha_7$	0.50 (0.12) **
<i>initfl25</i>	$\alpha_8$	0.45 (0.15) **
<i>SPEI6 * sdi</i>	$\alpha_9$	0.08 (0.01) ***
<i>SPEI6 * ln(basal area)</i>	$\alpha_{10}$	<−0.001 (<0.001) ***
Random effect		Estimate
<i>Tree level</i>	$b_i(\sigma)$	0.348 (StdDev)
<i>Autoregressive parameter</i>	$\varphi$	0.758
Residuals		StdDev
	$\varepsilon_{ij}(\sigma)$	0.484
<i>Number of trees</i>	$N_{tree}$	78
<i>Observations</i>	$N_{bai}$	2250
<i>AIC weight</i>		0.295

**Table 3.** Parameter estimates and standard errors (*se*) of the best models for resistance (left), recovery (center), and resilience (right) resulting from the multi-model inference.  $\alpha$  are the regression coefficients of the fixed covariates,  $b$  represents the random intercept,  $\varepsilon$  is the error term, and  $N$  stands for the number of trees, respectively the number of observations. Significance levels: \*\*\* = 0.001, \*\* = 0.01, ° = 0.1.

Fixed Effect Parameter	Resistance		Recovery		Resilience	
	Fixed Effect Variable	Estimate (se)	Fixed Effect Variable	Estimate (se)	Fixed Effect Variable	Estimate (se)
$\alpha_0$	<i>intercept</i>	−0.86 (0.44) °	<i>intercept</i>	0.31 (0.08) ***	<i>intercept</i>	−0.19 (0.14)
$\alpha_1$	<i>ln(basal area)</i>	0.04 (0.07)	<i>year</i>	0.47 (0.04) ***	<i>year2015</i>	−0.09 (0.18)
$\alpha_2$	<i>year2015</i>	2.15 (0.51) ***	<i>cvarbai</i>	−0.69 (0.20) ***	<i>cvarbai</i>	−1.08 (0.35) **
$\alpha_3$	<i>strudiv</i>	0.26 (0.21)			<i>strudiv</i>	0.39 (0.21) °
$\alpha_4$	<i>ln(basal area) * year2015</i>	−0.33 (0.08) ***			<i>year2015 * cvarbai</i>	1.43 (0.44) **
<i>Tree level</i>	Random effect	StdDev	Random effect	StdDev	Random effect	StdDev
	$b_i(\sigma)$	0.07	$b_i(\sigma)$	0.13	$b_i(\sigma)$	0.10
<i>Number of trees</i>	Residuals	StdDev	Residuals	StdDev	Residuals	StdDev
	$\varepsilon_{ij}(\sigma)$	0.31	$\varepsilon_{ij}(\sigma)$	0.28	$\varepsilon_{ij}(\sigma)$	0.35
<i>Observations</i>	$N_{tree}$	78	$N_{tree}$	78	$N_{tree}$	78
	$N_{rt}$	156	$N_{rc}$	156	$N_{rs}$	156
<i>AIC weight</i>		0.729		0.716		0.409



**Figure 5.** Growth responses of *N. spruce* to droughts in 2003 (a) and 2015 (b). Each gray line represents the relative growth course of the spruce trees in a two-year period before the drought (PreDr; considered as a reference line = 1.0), during the drought (Dr), and a two-year period afterwards (PostDr). The bold black line shows the average growth response of all trees for the respective drought event. The vertical gray line highlights the drought event, whereas the dotted green line delineates a reference line based on the growth in the pre-drought period.



**Figure 6.** Predictions for resistance (a), recovery (b), and resilience (c) for the 2003 and 2015 drought events based on the best models. The blue, respectively the red, zone around the predicted course

indicates the 95% confidence interval. Note the different scale for resistance. For resistance and resilience, the predictor *strdiv* (structural diversity), included in the best model, was set to mean, while other variables were predicted independently. Effects of different levels of structural diversity are not presented here since this predictor was not significant in the models ( $p > 0.05$ ).

#### 4. Discussion

Due to the combination of repeated surveys, a broad range of treatments, and detailed climate data, the permanent spacing–thinning experiment FFB612 in a planted N. spruce forest provided an appropriate setting to examine if a tree's past affects growth, particularly in years with drought. We applied linear mixed effect models that included predictors describing climate conditions, different management approaches, and the current competitive situation aimed at helping to improve forest management guidelines. We found that (i) larger trees were more climate-sensitive, (ii) that greater structural heterogeneity in a tree's vicinity was beneficial for both its growth and drought resistance, respectively resilience, (iii) high past variation in competition negatively affected current growth, and (iv) high past growth variation caused less recovery from drought.

##### 4.1. Relationship between Climate, Growth, and Tree Size

In the past, conifers were planted extensively throughout Europe, preferably on fertile sites, to meet the demand for timber [29]. The FFB 612 permanent thinning trial is a typical high-yield spruce site in the foothills of the Alps [63]. Our results highlighted the relationship between climate and growth at this site. As expected, the trees grew better with a good water supply than with deficiency. Based on the Standardized Precipitation Evapotranspiration Index (SPEI6 August) and growth patterns of our sampled trees, we identified 2003, 2015, and 2018 as years with major drought events. These are considered the most severe droughts in Central Europe in recent decades [106–108]. Our analysis for the droughts in 2003 and 2015 proved once again that spruce could be considered a drought-sensitive tree species. Its comparatively high susceptibility to drought has already been highlighted in several studies across Central Europe, supporting the general assumption that spruce is inferior to predicted climatic changes [109–112]. This is particularly evident in stronger growth reductions, respectively lower drought resistance, in comparison to other species [19,28] and was confirmed for different elevations [113] and drought levels [114]. In the aftermath of the 2003 drought, our analysis showed that most trees barely recovered or even continued to decline in growth. The lack of recovery in the first two years after may be due to severe stress. Such slow recovery of diameter growth was previously observed under artificial drought stress induced by throughfall exclusion experiments [115] and was linked to potential non-reversible tissue damages [116]. In contrast, the picture for 2015 was the opposite, with trees appearing to recover quickly, and many even exceeding their pre-drought growth levels. The latter is consistent with the findings of Pretzsch et al. [19] in pure stands and Zang et al. [28] in mixed mountain forest stands, who also observed a rapid growth recovery. A possible explanation of a strong growth decline and a subsequent fast recovery could be attributed to the isohydric character of spruce [13,117]. It has strong stomatal control and, therefore, reduces its water consumption early when droughts occur [117,118]. This preventive strategy can be beneficial during shorter drought periods, as it allows drought-related damage to be avoided and enables a rapid recovery [19,118]. However, this strategy may prove to be detrimental during prolonged droughts, as the trees may already close their stomata while the water supply is still sufficient, making them vulnerable to carbon starvation [118]. Consequently, the severity and the duration of the drought in 2003 may be the reason for the more pronounced growth decline in comparison to 2015.

Our models revealed that tree size affected the climate-growth relationship. Larger trees were more sensitive to climate than smaller ones. This complies with Zang et al. [15], who found a more pronounced relationship between annual growth and summer climate in larger spruce trees. In terms of drought response, our results differed. While trees declined

in growth in 2003 regardless of tree size, the opposite was true in 2015. The larger the trees were in 2015, the more their growth declined. Similar results were obtained in the same study region for pure as well as mixed stands of N. spruce [17,119]. Gillerot et al. [120] also found significant negative effects of tree size on drought responses, especially for N. spruce. This is also coherent with the findings of a global study by Bennett et al. [121] that large trees suffer most from drought, leading to higher mortality risk [16,122]. An increase in direct solar radiation, higher wind speed, and, thus, higher evapotranspiration of taller trees may contribute to a more pronounced drought sensitivity [123]. Another explanation is provided by the limitation-caused matter partitioning (LCMP) hypothesis, which states that light limits growth under nutrient-rich conditions, leading to a size-asymmetric competition among trees. However, this may change to a size-symmetric competition when water, not light, is limiting in dry years. Then, resources are allocated more symmetrically among trees, resulting in a proportionally greater growth reduction for tall trees [17,78].

Mérian and Lebourgeois [124] found no differences between size classes in N. spruce in dry years, but they did in more shade-tolerant species, such as silver fir (*A. alba*) or European beech (*F. sylvatica*). In contrast, a different pattern was observed in Italian oak (*Q. frainetto*), with smaller trees being more affected by drought [125]. This underlines the importance of tree size in relation to the respective tree species. Moreover, the size of the trees themselves and the size distribution of trees in the direct vicinity were what mattered in our study. Our models for growth (1992–2020), resistance, and resilience indicated a positive effect of a wider diameter distribution within the vicinity of the trees, confirming that in addition to tree size, a less uniform stand structure can be beneficial for growth in drought years [126] and for stand productivity in general [127].

#### 4.2. Influence of Past Management Strategies on Growth and Drought Response

In recent studies, it has been argued that in the tree ring pattern, and in the crown and root morphology, the ecological memory of a tree is stored and thus reflected [53,54,128]. Since stand density is an important growth determinant [39], and thinning intensity and frequency are known to shape the pattern of ring width and wood density [48,129], we assumed that the management history is also stored in the ecological memories of trees. Our results confirmed that past management codetermined growth and response to drought. High fluctuations in past competition impaired growth, and the more the trees oscillated in their past growth, the weaker was their recovery and growth in the present. In terms of resilience, different response patterns were observed. While high growth variation was strongly negative in 2003, no such trend was noted for 2015. Bose et al. [130] also found effects of past growth variability on the drought response of Scots pine (*Pinus sylvestris*) along a latitudinal gradient across Europe. They showed that a high variability in growth in the ten years prior to drought affected resilience negatively. Pretzsch [83] made similar observations for N. spruce and E. beech in a mixed forest stand in the same region as FFB 612. This study showed that the inclusion of past growth metrics greatly improved model predictions of diameter growth in years with dry conditions. In particular, strong inter-annual growth variations were found to be detrimental to both species in the long-term. It was hypothesized that these effects were due to changing growing conditions and, thus, to a greater need for photosynthates for physiological and morphological acclimation. This could lead to a depletion of the trees' reserve pools and, therefore, to a reduced recovery from drought stress [53,83].

Several studies have already examined the effect of thinning on drought responses aimed at increasing resilience or resistance [45–47]. For instance, Sohn et al. [49] found that in S. pine stands in Germany, heavy and frequent thinning promoted recovery from drought, especially in recently thinned stands. Kohler et al. [47] observed that N. spruce trees with more growing space recovered faster and that these effects were still present even 10 years after the last intervention. Further, it has been shown that these benefits decrease with time since the last management activity [131]. Others also mentioned the positive effects of reduced stand densities [18,46], including unevenly structured, mixed stands [20,132].

Particularly for trees growing at dry sites, low stand densities seemed beneficial [45,133] as they helped to reduce the climatic sensitivity of the remaining trees [134,135]. In addition, Giuggiola et al. [42] recommended reducing stand density for isohydric tree species, such as *N. spruce*, to improve the water balance when trees occur near their ecological limit. Such positive effects of lower stand densities on drought response were observed at both the tree [46,47,114] and the stand level [18,136].

Contrary, Martínez-Vilalta et al. [137] observed for *S. pine* that fast-growing trees were more affected by drought, in turn suggesting the benefits of denser stands with slower growth rates. Low stand densities may also thwart the beneficial shading effects on smaller trees [17] and may harm the stand climate. Accelerated wind speed and intensified direct solar radiation [40] may lead to a reduced soil humidity [138] as well as higher evapotranspiration [51]. A widely open canopy could further promote the herbaceous understory [52] and, thus, increase the competition for water in dry regions, which may negatively affect regeneration and forest structure in the long-term [139]. Besides years with extreme climatic conditions, thinning in monospecific conifer stands was only found to accelerate short-term growth and even to be detrimental to long-term volumetric growth. This was particularly evident on fertile sites [140], such as FFB 612.

Next to thinning strategies during the later stages of forest development, the future growth course is already modulated by the initial spacing pattern [141]. Low competition in the early stages of development may cause rapid growth but also an early culmination. In contrast, there are the so called “latecomers”, i.e., trees that started growing slowly, but which accelerated their growth later [142]. Our study highlighted the importance of considering initial spacing for growth and confirmed that trees with greater initial spacing, respectively low or no competition, experience enhanced growth early on. However, as the model indicated, the overall highest *bai* was achieved at the moderate spacing distance, not the widest.

#### 4.3. Methodological Considerations

The assessment of the competition development of every single tree was based on a method we termed “pairing.” We matched the cored trees from the buffer zone with the corresponding trees from the plot based on the similarity of growth patterns. Competition metrics were derived from the trees within the plots and assigned to the cored trees. Thus, annual growth and competition data were acquired from different trees, which must be considered in terms of the generalizability of our results. We relied on this procedure because coring may affect future tree growth, and thus future studies at the permanent spacing–thinning trial. In our study, we modeled tree growth and drought responses in dependence on the basal area of each tree. However, it has recently been shown that the crown structure is also an important growth determinant [143]. Thus, if crown morphology had been surveyed more than once, it also could have been included in our modeling approach. It was necessary to account for edge bias at the plot boundaries to determine the competitive situation. We applied a toroidal shift to extend the same planting pattern across the boundaries and provide a bias-free competition estimate. We dismissed other possible techniques, such as mirroring the plots [82], as these methods might provide over-density.

Due to the limited sample size and the fact that only cores could be taken from the buffer zone, our study is subject to certain limitations. Nevertheless, because of the elaborated study design of FFB 612, we were able to answer our initial question of whether a tree’s individual past, shaped by its silvicultural treatment history, influences its current growth and drought response. For further studies, we propose to include a site gradient and extend the design to additional tree species to verify our initial findings.

#### 4.4. Consequences for Silvicultural Treatment

Although the conversion of coniferous, even-aged monocultures to more diverse mixed forests has been in the focus of forest research for decades [144–147], large parts of Central European forests are still dominated by conifers such as *N. spruce* [30,148], e.g.,

55% share of conifers in Germany [31]. Due to high susceptibility to pests, windthrow, and drought, ongoing climate change is increasingly becoming a problem for forestry practices in these stands [32]. Admixing or replacing the stands with suitable tree species is often recommended in the long term [36,148] because of the lower risk of natural disturbances and, thus, lower economic uncertainties [149]. Therefore, silvicultural guidelines strive to convert destabilized monospecific forests into more stable, mixed forests [150], which is possible with appropriate management strategies, as simulation studies have recently shown [146,151]. However, viable options should also be available for forest owners aiming for a higher proportion of conifers on productive sites. In this regard, adaptive management strategies that try to increase the resilience of trees to stress events, particularly drought, will be crucial [152]. Strong thinning is often considered a promising measure to improve resilience [45,134]. However, the long-term memory effects of thinning intensity and frequency have been largely neglected in the past. In contrast, recent studies have demonstrated that prior management, respectively the ecological memory, is substantial for tree growth under drought [44,53,83]. Our results also indicated that the trees' individual past (e.g., initial spacing, variation in growth, and competition) co-determine the growth and drought responses of trees. In more detail, our results implied that large fluctuations in growth or stand density may be detrimental to drought recovery at the tree level, which is consistent with stand-level results for the same study site [153]. We hypothesize that constant and regular interventions may be favored over irregular ones, confirming earlier findings by Pretzsch [140] that continuous, moderate stand density reductions may stabilize tree and stand growth. However, further research is required to strengthen these initial findings.

Possible further measures to improve forest resilience include increasing the vertical and horizontal structural diversity, as structurally diverse forests are considered to be more resistant [36]. This is supported by our finding that higher structural diversity improved resilience and resistance. Since small trees are less susceptible to drought, maintaining a healthy understory, and thus promoting structural heterogeneity, could compensate for growth losses in larger trees [17] and should be considered in forest management strategies [122]. This accords with the theory of latecomers and quick starters by Pretzsch [142], which suggests combining trees from different social positions within a stand to ensure a stable stand growth in the long-term. Thus, suppressed trees that initially grew slowly (latecomers) may replace quick starting trees that decline in growth and maintain a continuous structure over time. To achieve high levels of size-class diversity, thinning from above has shown to be promising [126,154] and has been linked to increased forest resilience and improved economic efficiency [155].

**Author Contributions:** Conceptualization, H.P.; methodology, G.S., T.H., E.U. and H.P.; software, G.S.; formal analysis, G.S. and T.H.; data curation, G.S.; writing—original draft preparation, G.S.; writing—review and editing, T.H., E.U. and H.P.; visualization, G.S.; supervision, H.P. All authors have read and agreed to the published version of the manuscript.

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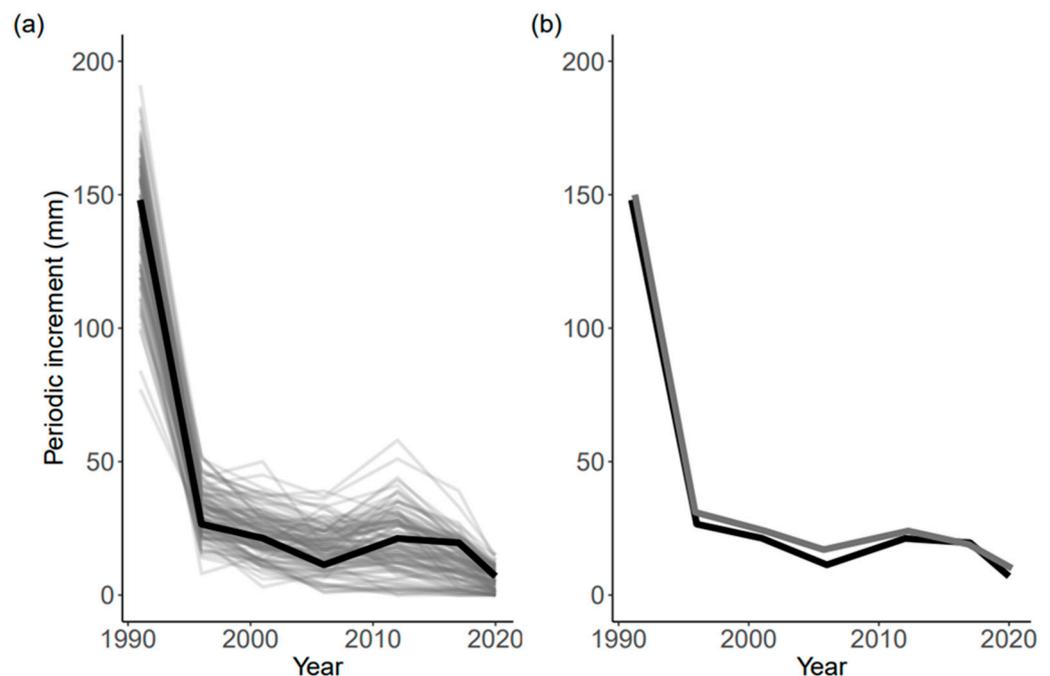
**Data Availability Statement:** Not applicable.

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**Conflicts of Interest:** The authors declare no conflict of interest.

## Appendix A. Description of the Pairing-Process

To determine how the individual past of a tree affects its growth, particularly its drought response, we relied on the one hand on periodic surveys that give information about the competition and related changes, and on the other hand on annual growth data derived from dendrochronological measurements. However, competition data were gained from trees within the plots, whereas annual growth data was obtained from trees from the buffer zone. Consequently, a procedure was required to combine the data. Thus, we established a procedure called pairing, which assumes that a tree from the buffer zone with the same growth trajectory as a tree from the plot have the same competitive history. For this process, we first derived periodic increments from each tree within the plots based on the  $dbh_{1.3}$  measurements from the surveys. In the next step, we used the annual increments of each cored tree and aggregated those into periodic increments that matched the survey years. Then, we compared the growth trajectories of each cored tree with all trees from the corresponding plot. The lowest sum of squares calculated between the trees' growth trajectories resulted in a match. Based on that match, the tree data gained from the surveys were extracted and assigned to the respective cored tree. Subsequently, these data were used for further calculation of competition indices. Thus, the pairing process was used to determine the similarity between growth trajectories of cored trees from the buffer zone and trees from the plot to derive the individual competition history of each tree. An explanatory result from the pairing process is illustrated in Figure A1.



**Figure A1.** (a) Comparison of the periodic growth trajectories during the pairing process. The cored tree from the buffer zone is marked black, while the gray lines represent the corresponding trees from within the plot. (b) Best match between the cored tree (black) and the respective tree from the plot (gray) based on the lowest sum of squares. The high periodic increment at the beginning reflects the growth of the first 22 years of life until the first survey.

## Appendix B. Quantification of Drought Responses

For the calculation of the indices that try to quantify drought responses, we used raw annual basal area increments ( $cm^2$ ) and detrended, dimensionless tree-ring series as recommended by Schwarz et al. [57]. For the detrending procedure, we compared different methods using the interactive detrending option of the package *dplR* [96]. Finally, we applied a smoothing spline with a 50% frequency response cut-off at  $2/3$  of series length on each *bai* series [156]. Detrending procedures attend to remove long-term biological growth

trends, e.g., caused by age [68,156]. However, we relinquished the detrended version since all trees in our experiment had the same age. Besides, we were primarily interested in the effects of each tree's individual past, e.g., thinning intensity and frequency, and detrending can cancel out these effects [157]. Further, comparisons between the same indices, using detrended and raw basal area increments, revealed high correlations ( $r \geq 0.9$ ). The same was observed in a similar study, where the detrended tree-ring series were also excluded from further analysis [114]. Before and after each identified drought, there was at least a two-year span with normal or wet climatic conditions, considered as favorable for growth. Therefore, we chose a period length of two years for all droughts. However, the 2015 drought was shortly followed in 2018 by another drought, which led to the problem that the 2015 post-drought period was also the potential pre-drought period of 2018. Further, water stress has been shown to have significantly affected growth in the following 1–2 years, potentially making it vulnerable to repeated drought [158]. Thus, the pre-drought period of 2018 and the growth response to the drought in 2018 itself were possibly influenced by the preceding drought stress. Taking this into account, we excluded 2018 from our modeling approach.

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